

PARALLEL AND CONVERGENT EVOLUTION IN FERNS

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WHATEVER the details of its technique, evolution is accepted by the world as the general process by which the countless kinds of living things have been derived from comparatively uniform remote ancestors, and finally perhaps from one single living thing. This has been in general a process of differentiation. It has been so also in detail, as each kind of living thing originated from a more or less different parental kind or species. We are so used to regarding evolution as a process of differentiation that if a botanist or zoologist be asked as to the occurrence of convergent evolution, by which similar or apparently identical creatures are evolved from different ancestors, he is likely to reply that it is theoretically possible, but that he knows of no recognized instance. He may add that if such a procedure did occur in nature, we might not recognize it, but that it would be interesting if we could demonstrate it.

However, as a general proposition, some measure of convergent evolution is not only not rare, but is familiar, if one will but consider what one knows. Dry lands the world over receive immigrants from more humid lands, which undergo similar modification in adaptation to the dry climate. Dry-land plants of the most diverse ancestry thus evolve small, harsh leaves. Many Euphorbiaceae have evolved the form and much of the structure more familiar in the cacti. Dwarf species inevitably lose some of the structures of their larger ancestors, with loss of size. The most universally familiar example of this phenomenon is the loss of structure by parasites, and the resulting resemblance of plants quite regardless of the differences between their ancestors. Plants of many families have undergone in common the loss of leaves and of chlorophyll in becoming parasites. This evolution is convergent or parallel; there is no essential difference. The possibility that present resemblance may blind us to diverse ancestry is shown by the fact that we hold our predecessors of a few years to have been deceived in this way. We recognize more families of parasites than were known some years ago, because we believe that the old families contained unrelated, even if similar, elements.

The ferns are better known, as to their geography and their real affinities, than is any other group of similar size. None is a parasite, and few are dry-country plants. In the light of our present understanding of the relationships of the genera, we now recognize among them numerous instances of parallel and convergent evolution. As recently as the period when the elders among us began to study ferns, their classification by Sir William Hooker was accepted with little question throughout the world.

As Sir William was one of Darwin's influential supporters, this should not have been the expression of a purely pre-Darwinian viewpoint. The Synopsis Filicum of Hooker and Baker recognized 58 genera of Polypodiaceae. One of the greater of these was *Acrostichum*, including almost all ferns with the sporangia spread over the backs of the fronds, — not in discrete clusters, called sori.

Of the 172 species of *Acrostichum* in the 1874 edition of Synopsis Filicum, only (1) *A. aureum* retains to-day that generic name; it is probably a relative of *Pteris*. *Acrostichum pteroides*, now *Neurosoria pteroides* (2), is a little known Australian species related to *Cheilanthes*, perhaps belonging in that genus. *Acrostichum requiniana* is now (3) *Taenitis requiniana*, an imperfectly acrostichoid derivative of the widespread *T. blechnoides*.

Acrostichum apiifolium, endemic in the Philippines, is a descendant of *Dryopteris*,¹ now called (4) *Psomiocarpa apiifolia*, a name given in 1849 but rejected by Hooker and Baker. The Cuban *A. aspidioides* is a very similar independently derived dryopterid fern, now called (5) *Atalopteris aspidioides*. For *A. auritum*, the name (6) *Stenosemia aurita*, given in 1836, has been restored; it is descended from *Dryopteris* through an intermediate genus, *Heterogonium*. Also derived from *Dryopteris*, but from a different part of the genus, is (7) *Quercifilix zeilanica*, called *Acrostichum quercifolium* by Hooker and Baker. Baker later described as *Acrostichum* three species (*A. celebicum*, *A. exsculptum*, and *A. oligodictyum*) now recognized as (8) species of *Dryopteris* (or better, of *Cyclosorus*), all imperfectly acrostichoid in fruit. *Acrostichum Harlandii* and *A. taccaefolium* are species of (9) *Hemigramma*, derived from *Tectaria*, of more remote dryopterid origin.

Acrostichum scandens is now (10) *Stenochlaena palustris*, not clearly related to any other fern here mentioned. *Acrostichum sorbifolium* has been called *Stenochlaena* by some more recent authors, but is better distinguished as (11) *Lomariopsis*. Confused with *A. scandens* in the Synopsis was a very different fern, (12) *Teratophyllum aculeatum*; except that the resemblance is not sufficient to justify Hooker's confusion, we would have here a fine illustration of generically distinct ferns masquerading as specifically identical. *Acrostichum Blumeanum* is now a (13) *Lomagramma*. *Acrostichum articulatum* and *A. Wilkesianum* have also been called *Lomagramma*, but are better distinguished as (14) *Arthrobotrya*. The evolution of these four or five genera has been so convergent that there is to-day no agreement as to their real affinities; but it is agreed that *Stenochlaena*, *Lomariopsis*, *Teratophyllum*, and *Lomagramma* are distinct from one another as well as from *Acrostichum*.

A considerable number of former *Acrostichum* species are now regarded

¹ To avoid a less familiar name, I use *Dryopteris* here in the sense of Christensen's Index Filicum.

as (15) *Bolbitis*, a pantropic genus. An oriental relative of *Bolbitis* is (16) *Egenolfia*, represented in the Synopsis as *A. appendiculata*. Roughly half of the *Acrostichum* species of the Synopsis are now (17) *Elaphoglossum*, a very large genus in all warm countries. Derived from *Elaphoglossum* are (18) *Microstaphyla* and (19) *Rhipidopteris*, each represented by one species of *Acrostichum* in the Synopsis. These five genera have in common a striking spore character, indicating that they are related, mutually and to other ferns recently mistakenly placed in *Dryopteris*.

Acrostichum bicuspe is (20) *Cheiropleuria bicuspis*, a Malayan fern so peculiar that it has been proposed to make it a family by itself. Related to it, however, is (21) *Christiopteris tricuspis*, *A. tricuspe* of the Synopsis. *Acrostichum spicatum* and *A. platyrhynchos*, now called (22) *Belvisia* (or *Hymenolepis*), may be a third surviving branch of the same old group.

Of the polypodioid ferns, *Acrostichum axillare* is (23) *Leptochilus axillaris*, which is so deceptively like *A. lanceolatum*, a (24) *Dendroglossa*, that botanists as keen as Christensen and Ching have been unable to see that they are generically distinct. Under *A. variabile*, Hooker and Baker combined one or more species of *Dendroglossa* with (25) *Leptochilus*² *decurrens*, which I am sure is of independent immediate ancestry. *Acrostichum rigidum* is (26) *Photinopteris speciosa*, derived through *Aglaomorpha* from *Microsorium*, which is the immediate parent of *Leptochilus*. *Acrostichum drynarioides* is now (27) *Merinthosorus*, likewise derived from *Aglaomorpha*.

In running through this list, I have overlooked three American genera, (28) *Trachypteris*, (29) *Neurocallis*, and (30) *Polybotrya*.

Platycterium is also perfectly acrostichoid in its fructification, but for other reasons Hooker and Baker held it generically distinct.

It will help to show the diversity of origin of the foregoing list of genera if they be now tabulated in their most recent systematic arrangement.

PTERIDACEAE

<i>Taenitis requiniana</i>	<i>Acrostichum requinianum</i>
<i>Neurocallis praestantissima</i>	<i>A. praestantissimum</i>
<i>Acrostichum aureum</i>	<i>A. aureum</i>
<i>Neurosoria pteroides</i>	<i>A. pteroides</i>
<i>Trachypteris aureo-nitens</i>	<i>A. aureo-nitens</i>

ASPIDIACEAE

<i>Polybotrya osmundacea</i>	<i>Acrostichum osmundaceum</i>
<i>Bolbitis serratifolia</i>	<i>A. serratifolium</i>
<i>Egenolfia appendiculata</i>	<i>A. appendiculatum</i>
<i>Lomariopsis</i> spp.	<i>A. sorbifolium</i>
<i>Teratophyllum</i> spp.	<i>A. sorbifolium</i>
<i>Arthrobotrya articulata</i>	<i>A. articulatum</i>
<i>Lomagramma</i> spp.	<i>A. Blumeanum</i>

² *Leptochilus decurrens* is the name in present use for this species, but it is improper because the species is of different immediate ancestry from *L. axillaris*, the type of *Leptochilus*. A new generic name is provided for it in my *Genera Filicum*, now in press.

<i>Elaphoglossum</i> spp.	<i>Acrostichum</i> spp.
<i>Microstaphyla furcata</i>	<i>A. bifurcatum</i>
<i>Rhipidopteris peltata</i>	<i>A. peltatum</i>
<i>Psmiocarpa apiifolia</i>	<i>A. apiifolium</i>
<i>Atalopteris aspidioides</i>	<i>A. aspidioides</i>
<i>Stenosemia aurita</i>	<i>A. auritum</i>
<i>Hemigramma taccaefolia</i>	<i>A. taccaefolium</i>
<i>Quercifilix zeilanica</i>	<i>A. quercifolium</i>
BLECHNACEAE	
<i>Stenochlaena palustris</i>	<i>Acrostichum palustre</i>
POLYPODIACEAE	
<i>Cheiropleuria bicuspis</i>	<i>Acrostichum bicuspe</i>
<i>Christiopteris tricuspis</i>	<i>A. tricuspe</i>
<i>Belvisia (Hymenolepis) spicata</i>	<i>A. spicatum</i>
<i>Platynerium</i> spp.	<i>Platynerium</i> spp.
<i>Leptochilus axillaris</i>	<i>Acrostichum axillare</i>
<i>Leptochilus decurrens</i>	<i>A. variabile</i> , in part
<i>Dendroglossa minor</i>	<i>A. minus</i>
<i>Merinthosorus drynarioides</i>	<i>A. drynarioides</i>
<i>Photinopteris speciosa</i>	<i>A. rigidum</i>

I may not apologize for the length of this list of names, uninteresting to the pteridologically illiterate, even if musical, because the length of the list is the point I emphasize, and have repeated for the sake of emphasis. The list might be made much longer, if, instead of confining myself to Hooker, I went back to Swartz, and to Linnaeus, whose definition of *Acrostichum* was substantially the same as Hooker's. Including their species, the number would have been more nearly fifty of to-day's genera, almost all representing the same kind of convergent evolution.

The acrostichoid fructification is usually associated with the evolution of dimorphic fronds, — different vegetative and fertile fronds, — the fertile ones usually restricted in area, longer-stalked, and shorter-lived. Some degree of dimorphism of fronds, or of parts of fronds, has been evolved independently along a considerably greater number of lines; but dimorphism did not happen to be a primary element in generic definition, and so the ends of the resulting phyletic series escaped combination on this ground.

The Synopsis Filicum maintains a genus *Gymnogramma* of about 100 species, including most ferns with the sporangia in extended lines along the veins and without protective covering, but not on the area between the veins, where their presence would have thrown the plants into *Acrostichum*. These hundred species are now distributed among the following 23 genera:— "*Dryopteris*," *Heterogonium*, *Woodsia*, *Athyrium*, *Ceterach*, *Asplenopsis*, *Syngamma*, *Craspedodictyum*, *Pterozonium*, *Coniogramme*, *Hecistopteris*, *Gymnopteris*, *Gymnogramma*, *Pleurosorus*, *Eriosorus*, *Bommeria*, *Anogramma*, *Trismeria*, *Pityrogramma*, *Loxogramme*, *Colysis*, *Sclligea*, and *Pleopeltis*. Because some of these genera include more than one independent instance of such evolution, because the Synopsis treats as genera (*Meniscium*, *Hemionitis*) some such series, and because of several

such cases unknown to its authors, the actual number of independent evolutionary series converging to the *Gymnogramma* type of fructification is again far more than thirty.

The feature in which parallel evolution has occurred in the largest number of cases is the loss of the indusium. Failure to recognize this by taking account of ancestry was responsible for the monstrous "genus" *Polypodium*; within restricted ranges, for such temporarily respected genera as *Phegopteris*, *Goniopteris*, and *Alsophila*. Presentation of individual cases would involve discussion of species rather than genera, and would require far more space than is available here.

Limiting myself to genera, I will close with two especially interesting cases.

The pair of genera *Cochlidium* and *Scleroglossum* present an exceptional case of convergent evolution. The former has ten named species in tropical America; the latter, seven, from Ceylon to Polynesia. They are tiny ferns with densely clustered thick, linear fronds, with one linear sorus on each side of the midrib in the upper part of the frond. They are so alike that care is required to distinguish the species in the two hemispheres. Their geographical isolation made their generic identity doubtful, but a detailed anatomical study by Goebel made him conclude that there was no sufficient ground for their separation. Before and after his study, I was forced to the same conclusion; the more reluctantly the second time, because Goebel had also established the common descent of the American *Cochlidium* and *Xiphopteris*, and Maxon had previously shown that *Xiphopteris* was too intimately connected with its local neighbors, pinnate ferns called *Polypodium*, or preferably *Ctenopteris*, to require recognition as a genus. This established *Cochlidium* as a genus of American origin, and no other genus of demonstrable American origin was known in the Malay region.

And then, a New Guinea plant named "*Polypodium pleurogrammoides*" came to hand. Let its generic name be what it will (it can be *Nematopteris*, or *Grammitis*), it shares the characteristics of *Scleroglossum* and *Grammitis*, and illustrates the derivation of the former from the latter. The proof is provided by microscopic features of identity, but is sufficient. *Cochlidium* is descended from pinnate ferns; *Scleroglossum* from a genus with simple fronds. But convergent evolution produced genera so identical that neither Goebel nor I could find a satisfactory distinction, though antecedent probability made us expect one. Christensen has later found a second microscopic difference.

Phyllitis Scolopendrium, longer known as *Scolopendrium vulgare*, the "hart's tongue fern," occurs well around the North Temperate zone. Its sorus is "double"; that is, each of two neighboring veins produces a long sorus, on the side facing the other vein, and the indusia are broad enough either to meet, or to come near enough to doing so that the result looks like one sorus. The genus is derived from *Asplenium*. The North Amer-

ican *Asplenium pinnatifidum*, which suggests *Scolopendrium* so strongly that Diels transferred it to that genus, may represent its parentage in *Asplenium*. *Phyllitis* is clearly of northern origin, and is probably not at all ancient.

Scolopendrium Durvillei Bory was described from the New Guinea region. Though misunderstood by Baker and made the basis of another genus, *Diplora*, it has exactly the soral character of *Scolopendrium*. Its approximate ancestor in *Asplenium* is *A. epiphyticum*, not more nearly related to *A. pinnatifidum* than it must be as an *Asplenium*. If not *Asplenium*, *Scolopendrium* and *Diplora* must be two genera, distinguishable by description solely by the base of the lamina, cordate in one, cuneate in the other. This would be unsatisfactory if it were the whole story.

But we know now not merely two, but six instances in which convergent or parallel evolution has produced from *Asplenium* the sorus of *Scolopendrium*:

Asplenium Scolopendrium L.

Scolopendrium Durvillei Bory, the preferable name of which seems to be *Asplenium scolopendropsis* F. v. M.

Scolopendrium Delavayi Franch., preferably *Asplenium Delavayi*.

Scolopendrium cardiophyllum Hance, made a distinct genus, *Boniniella* by Hayata, but better treated as *Asplenium*.

Antigramma Presl, of Brazil, usually called *Scolopendrium*.

Schaffneria nigripes Fée, of Mexico, known also as *Scolopendrium* and *Phyllitis*.

If a summary be desired:

Parallel and convergent evolution are really common phenomena in ferns.

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